A Review of the Living Tectibranch Snails of the Genus *Volvulella*, with Descriptions of a New Subgenus and Species from Texas

BY

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(21 Text figures)

THIS STUDY BEGAN with an attempt to identify some specimens of *Volvulella* from Galveston, Texas, which proved to belong to an undescribed species more similar to one from the west coast of North America than to any hitherto known from the Atlantic. It is proposed as the type of a new subgenus. Snails of this genus live subtidally and to several hundred meters depth in tropical and warm temperate oceans throughout the world. They are local in occurrence and rarely abundant. It is not surprising therefore that the limits of species variation are poorly understood. There has also been confusion of the generic nomenclature, and the family to which they belong is still a moot question. The most recent monograph of the genus is by PILSBRY (1893). Monographic treatment of the whole genus has not here been attempted, since sufficient material was not available. Effort was concentrated on differentiating the species on American shores. A synonymy is given of the species of the eastern Atlantic, probably representing only one biological species, and a list of the nominal species of the western Pacific and Indian Oceans is appended, with comments. Five species named by DALL (1919) from the west coast and one from the east coast (DALL, 1927) were never illustrated. Opportunity to study this problem at the U. S. National Museum allowed me to make camera lucida drawings of the type specimens of DALL's nominal species. Measurements were made with an ocular micrometer, and are possibly more exact than those given by DALL. Most of DALL's type material was series of badly worn specimens, from which he evidently made composite descriptions. Lectotypes are here designated for each lot.

I am obliged to the Bureau of Commercial Fisheries of the U. S. Fish and Wildlife Service, Galveston, and especially to Messrs. Robert Temple, Clarence Fisher and Charles Guice for the material from the western Gulf of Mexico. The many courtesies of Dr. Harald Rehder, Dr. J. P. E. Morrison and Dr. Joseph Rosewater, while I worked at the U. S. National Museum, are gratefully acknowledged. This study was supported in part by National Science Foundation Grant GB 2753.

This genus has sometimes been placed in a separate family (Volvulidae, LOCARD, 1892; Rhizoridae DELL, 1956). After an extensive study of the anatomy of *Volvulella persimilis* from Brazil, MARCUS & MARCUS (1960) concluded that tentatively this genus should be placed in the Retusidae.

Volvulella NEWTON, 1891

Volvula A. ADAMS *in* SOWERBY's Thesaurus Conchyliorum 2: 555. Type by SD of A. ADAMS, 1862, Ann. and Mag. Nat. Hist. Ser. 3, vol. 9, p. 154, *V. acuminata* (BRUGUIÈRE) (= *Bulla acuminata* BRUGUIÈRE, 1792). Not *Volvula* GISTEL, 1848, Naturgesch. Thierr. f. Höhere Schulen, p. viii (Diptera).

Volvulella NEWTON, 1891, British Oligocene and Eocene Mollusca, p. 268. Substitute name for *Volvula* A. ADAMS, 1850, hence with same type species.

Rhizorus MONTFORT, 1810 of authors, not of MONTFORT.

ARTHUR ADAMS (1850) did not designate a type from among the 5 species which he included in *Volvula*, proposed as a subgenus of *Bulla*, nor was there otherwise intrinsic fixation of the type. MENKE (1854) declared *Volvula* ADAMS to be a synonym of *Rhizorus* MONTFORT, citing as type *V. acuminata*, which species he admitted he did not have. Since the two generic concepts are not the same, his designation of type can not be valid for *Volvula* ADAMS. H. & A. ADAMS (1854) also denied the identity of these two concepts. Their choice of the Australian species, *V. rostrata* ADAMS (1850) as an "example" of the genus was not construed by them or any subsequent

author to be *per se* a designation of the type species, but it may have led BUCQUOY, DAUTZENBERG & DOLFUS (1886) to designate that species as type. In 1862 A. ADAMS designated the first species of his monograph of 1850 as type, the European *V. acuminata* BRUGUIÈRE. PILSBRY designated the same type in 1893, but neglected to indicate the basis for his type selection. All subsequent authors have erroneously adopted the type designation of BUCQUOY *et al.*

NEWTON (1891) renamed ADAMS' concept, thinking *Volvula* was a homonym of *Volvulus* OKEN, 1815. By modern concepts of nomenclature these are not homonyms, since they differ by gender as shown by the endings. Therefore PILSBRY (1893) rejected NEWTON's substitute name, but he overlooked the genus *Volvula* GISTEL, 1848, which does invalidate *Volvula* ADAMS, 1850.

Several authors have continued to use *Volvula* A. ADAMS for this group of snails (NICKLÈS, 1950; PRUVOT-FOL, 1954), although GRANT & GALE (1931) gave the valid argument for accepting *Volvulella.*

The genus *Rhizorus* MONTFORT, 1810 (Conch. Syst. 2: 339, and plate on opposite page) has been considered by several authors during the nineteenth century as applying to this group of snails, but most rejected it as representing some other genus or as a result of their subjective nomenclatural conservatism (H. & A. ADAMS, 1854; JEFFREYS, 1867; PILSBRY, 1893; DALL, 1889). The single species which MONTFORT included in his genus, and designated as type, *Rhizorus adelaidis,* was described as being as big as a grain of millet. It came from the island of Elba, Italy, but was thought probably also present in England. He refers to a figure in SOLDANI, a work not available to me, nor evidently to most writers who have studied the question. To show that MONTFORT's genus can scarcely apply to *Volvulella,* a tracing of his illustration of *R. adelaidis* is here reproduced (Figure 1). It has the apex broadly truncate, scarcely tapering, and widely umbilicate; the aperture extends well above the apex, and is not curved toward the columellar axis there. All of these characters contrast with *Volvulella,* which, though some variants may be spineless and minutely umbilicate, have the aperture curved distinctly if only slightly toward the shell axis. Moreover, there are much better candidates for MONTFORT's concept, from the area he indicated, than the single species of *Volvulella* which is generally recognized from there. His concept may apply to something like "*Cylichna conulus* DESHAYES" as described and figured by FORBES & HANLEY (1851, 3: 517; 4: pl. 114c, figure 7). GRAY (1847) early associated MONTFORT's genus with such forms.

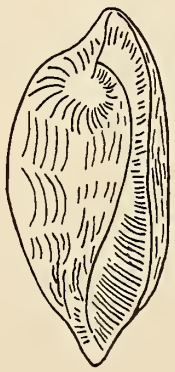

Figure 1

Tracing of figure of "*Rhizorus adelaidis*" from volume 1, page 338, MONTFORT, 1810

Several major works of recent years have adopted *Rhizorus* MONTFORT for this genus (e.g. WINCKWORTH, 1932; ABBOTT, 1954; POWELL, 1962). KEEN (1947) and PALMER (1958) have protested its use in this respect.

Snails of the typical subgenus have small shells (up to 9 mm long) which are tapering, ovate or subcylindrical. They are completely without intrinsic color, being light grey and translucent when taken alive, but soon turning snow white and opaque after "weathering" in nature. The aperture is narrow, elongate, rounded basally and extended the entire height of the shell. There is no columellar lamella or other apertural dentition. At its apical end the aperture bends over the apex of the shell, and the parietal wall here forms a spine which completely covers the apex, so that only the final whorl is visible. This, together with the non-determinate growth of the shell, makes it difficult to recognize juvenile shells as such, unless one has a large series available. The apical end of the aperture is almost or entirely as far advanced in the direction of growth as the rest of the outer lip. It is not deeply sinuate, and consequently extends as high as the tip of the spine in apertural view. There is a thin, colorless periostracum which is soon destroyed after death. Spiral sculpture of fine, incised lines, rather widely spaced, occurs at both ends of the shell (macro-spirals) in most species, and most (all?) have finer, closely set, wavy lines incised over the middle part of the whorl (micro-spirals). The micro-spirals are almost limited to the periostracum, and rarely evident on the even slightly weathered specimens. The shells are always imperforate basally, but a slight elevation of the narrow columellar lip from the whorl defines a furrow and minute pseudo-umbilicus.

Most characters show considerable variation within a species. The apical extent of the aperture and its bending

toward the columellar axis may vary even within specimens from one locality. This results in the spine varying from long and tapering to short and blunt, or in extreme cases, being replaced by a minute umbilicus at the apex. In worn shells the spine seems to undergo similar degradation, even if it were long and acute in the living animal. The spiral lines are variable in unworn shells of a species from one locality, and weathering rapidly degrades them. The basal lines are stronger and more persistent than the apical ones, and both are generally more so than the micro-spirals. The form may vary from oval to more elongate, perhaps within the growth of a single individual. But the shape of the shell seems to vary less than other characters within a species, and therefore is the most useful criterion at the species level.

Few species have special features which aid in identification, but examples are: the unusual thickness of the shell in *Volvulella paupercula* and *V. catharia*; the transverse riblets near the apex of *V. recta*; the tendency of the shells of *V. panamica* and *V. texasiana* to be stained with iron, and the peculiar apical sinus in the lip of these species; the apical ridge in *V. texasiana.*

At least 4 distinct groups of species are living today. The eastern Atlantic may have only one of the 4, but the western Atlantic, eastern Pacific and Indo-Pacific areas all contain very similar representatives of the other 3 species groups. Just how closely related these analogous populations are from the standpoint of taxonomy can not be definitely decided at present. The analogous species of each region differ so little, and then chiefly in their form, that a comparison of specimens from the several areas is the only convincing demonstration of their distinctness. Although only one species is generally recognized from the eastern Atlantic (Bucquoy *et al.*, 1882; Nicklès, 1950; Pruvot-Fol, 1954), other species have occasionally been recognized from there (Dall, 1889; Pilsbry, 1893). The following table summarizes the analogous species of the Atlantic and eastern Pacific Oceans. As my study of the populations of the Indian and western Pacific Oceans is based almost entirely on the literature, I have not included them in this table, but appended a list of the nominal species below.

Eastern Atlantic	Western Atlantic	Eastern Pacific
Subgenus *Volvulella s. s.*		
V. acuminata	*V. persimilis*	*V. cylindrica*
none?	*V. recta*	*V. californica*
none?	*V. paupercula*	*V. catharia*
Subgenus *Paravolvulella,* new subgenus		
none?	*V. texasiana*	*V. panamica*

Species of the Eastern Atlantic

Volvulella acuminata (Bruguière, 1792)

Bulla acuminata Bruguière, 1792, Encycl. Méth. vol. 1, prt. 2, p. 376, no. 9. Not figured. Type locality: not specified; evidently the Mediterranean, near northwestern Italy

Volvula cylindrica E. A. Smith, 1872, Proc. Zool. Soc. London p. 738, plt. 75, fig. 29. Not *V. cylindrica* Carpenter, 1864

Volvula smithii Pilsbry, 1893, Tryon's Man. Conch. 15: 233-234, plt. 26, fig. 65. New name for *V. cylindrica* Smith, 1871

Volvula acuminata var. *brevis* Pilsbry, 1893, Tryon's Man. Conch. 15: 235, plt. 60, fig. 11. Type locality: Northern Europe, Mediterranean

Volvula suavis Thiele, 1925, Wiss. Ergeb. d. deutsch. Tiefsee Exp. 17 (2): 238, plt. 31, fig. 20. Type locality: 16° 26.5′ S. Lat., 11° 41.5′ E. Long. (off Angola, Africa). He compared the single shell found with *V. acuminata*

There is variation in shape of this species, at least among the several lots from northern Europe of the Jeffreys collection in the U. S. National Museum. Larger specimens tend to be more elongate and more slender than smaller ones, which are more oval. The spine is elongate and acutely tapering. Completely spineless specimens were not found among the fresh, non-worn shells. Macrospiral lines occur at both ends, and faint microspirals are evident in many fresh shells. The eastern Atlantic shells always seem slightly more inflated than *Volvulella persimilis,* although the difference is very small, and requires actual comparison of specimens to demonstrate it adequately.

The range of *Volvulella acuminata* extends from Norway along the coast of Europe, including the Mediterranean, and south along the African coast to Angola (Nicklès, 1950). Pruvot-Fol (1954) lists it also from the Gulf of Suez at the head of the Red Sea, and indicates *V. oxytata* (Bush) and *V. persimilis* (Mörch) may be only varieties. She thought this species might be circumterrestrial, as did Melvill (1906).

Figure 2 (height 3.94 mm, diameter 1.69 mm) was drawn from one of 4 specimens on a card (USNM 175142) noting one of these shells was drawn as figure 1 of plate 93 of Jeffreys' "British Conchology." The exact locality of the specimens was not indicated, but it is presumably the British Isles. Figure 3 (height 4.06 mm, diam. 1.25 mm, USNM 175146) is one of a large lot from St. Magnus Bay, Shetland Islands. It illustrates a more cylindrical variant, with less acute spine. The specimen had been bored 3 times by some predaceous snail.

Species of the Western Atlantic

Volvulella persimilis (MÖRCH, 1875)

Volvula persimilis MÖRCH, 1875, Malak. Blätter 22: 179. Not figured. Type locality: "M. Antil." (Antilles). 1900, DAUTZENBERG, Mém. Soc. Zool. France 13: 155 - 156; plt. 9, fig. 10

Volvula oxytata BUSH, 1885, Trans. Conn. Acad. Sci. 6 (2): 468; plt. 45, fig. 12. Type locality: off Cape Hatteras, N. Car. in 7 to 17 fathoms

Volvulella mörchi DALL, 1927, Proc. U. S. Nat. Mus. 70: 22. Not figured. Type locality: off Georgia, U. S. Fish. Comm. Sta. 2415, 440 fathoms

Volvula ischnatracta PILSBRY, 1930. Proc. Acad. Nat. Sci. Philadelphia 82: 301; text fig. 1, p. 302. Type locality: Andros Bank, west of Middle Bight, about 12 miles within the western edge of the bank, in 3¼ fathoms (Bahamas)

This species is the western Atlantic counterpart of *Volvulella acuminata,* from which it is differentiated only by subtle differences of curvature of the whorl. The difference seems to be consistent when shells from the two sides of the ocean are compared side by side. The sculpture on both species is the same; prominent, broadly spaced spiral lines at both ends of the shell, and finer spiral lines between. To recognize *V. persimilis* as merely a subspecies of *V. acuminata* might be equally acceptable. *Volvulella persimilis* may not extend north of North Carolina, and thus the ranges of the two species do not, as presently known, meet in the North Atlantic. Numerous lots of *V. persimilis* are present in the U. S. National Museum from off Beaufort, North Carolina, and also from along the Florida Keys (J. B. Henderson) as well as smaller lots from Puerto Rico and Cuba. They range in depth from 15 to 209 fathoms. MARCUS & MARCUS (1960) described the anatomy of specimens from Brazil. Shells from Beaufort are long spined forms. Figure 4 (USNM 35871, height 3.50 mm, diam. 1.25 mm) is drawn from a specimen collected by the U. S. Fish Commission, Station 2112, in 15 fathoms off Cape Hatteras, North Carolina. It was sent to Dall by Bush. Whereas it may not be a paratype, it is at least an authentically identified specimen of what BUSH named *Volvula oxytata,* from the type locality. The terminal spiral lines are present on this specimen, but finer spiral lines on the middle of the shell were not seen, possibly due to slight weathering.

In the more southern part of the range of this species, there are specimens with shorter, blunted spines, and even no spine but a small apical umbilicus. Such forms occur in the same lots with acutely spined shells, but tend to be more abundant than the latter. It is probably intrinsic variation, rather than a common characteristic regularly evoked by a special environment. It was on such specimens that the species names *Volvulella moerchi* DALL and *Volvula ischnatracta* PILSBRY were based.

MÖRCH's original description of *Volvula persimilis* was based on a single specimen received from Krebs from the Antilles. His name is applied to the present species in part through a process of elimination, because his description best fits this species of those known to occur in the western Atlantic, and because he adequately differentiated it from the only other common shallow water species of the area (*V. recta* MÖRCH). The case for recognizing MÖRCH's name is much better than that for recognizing *V. acuminata* (BRUGUIÈRE). The original description [bracketed words inserted] of *V. persimilis* (MÖRCH) and my translation follow:

> "Differt a *Volvula angustata* A. AD. (Thes. XV 1850 p. 596 n 121, f 153) t. spiraliter subtilissime striata sub lente vix detegenda, solidiore; columella valida obliqua, plica crassa recta. Differt a praecedente [*V. recta* "D'ORB." MÖRCH = *V. acuta* D'ORB.] t. subcylindrica. Long 4½ mm; diam. 1¾ mm. Hab. M. Antill. (Krebs) spm. unicum."
>
> "Differs from *Volvula angustata* A. ADAMS (SOWERBY's Thesaurus Conchyliorum vol. 15, 1850, p. 596, No. 21, fig. 153) in that the shell is more solid, and spirally, very finely striate, the striae scarcely detectable under a lens; columella strongly oblique, with a coarse, straight lamella. It differs from the preceding [*V. recta* "D'ORB." MÖRCH = *V. acuta* D'ORB.] in that the shell is subcylindrical. Length 4½ mm, diameter 1¾ mm. Habitat M. [major? minor?] Antilles, a single specimen received from Krebs."

The figure of *Volvulella angustata* (A. ADAMS) (from the Philippines) referred to fits very well the brevi-spinous forms of this species in the West Indies. The aperture extends to the tip of the spine, thus differentiating it from *V. texasiana,* and the cylindrical form differentiates it from the bulbous *V. recta* and *V. paupercula.*

DAUTZENBERG (1900) redescribed and figured *Volvulella persimilis* from shells obtained at 10 fathoms off Venezuela. Although he argues that this species is distinct from *V. oxytata* (BUSH), the described and figured shells are quite within the range of variation of the species as here understood. MARCUS & MARCUS (1960) also thought these two names are synonyms.

Figure 5 is a drawing of the single specimen on which *Volvulella moerchi* DALL, 1927 was based (USNM 108268, U. S. Fish Commission, Station 2415). The shell is very worn, with the spine completely broken off and the outer lip badly damaged. It is chalky and opaque, showing no sculpture: height 3.68 mm, diam. 1.55 mm (DALL stated: Height 3.5; diameter 1.25 mm.). This specimen may have been accidentally present in the 440 fathom station where it was taken. DALL made no mention of depth in his description, but "440 fms." is on the label. He noted it "is nearest *V. persimilis* MÖRCH but is smaller and not spirally striated."

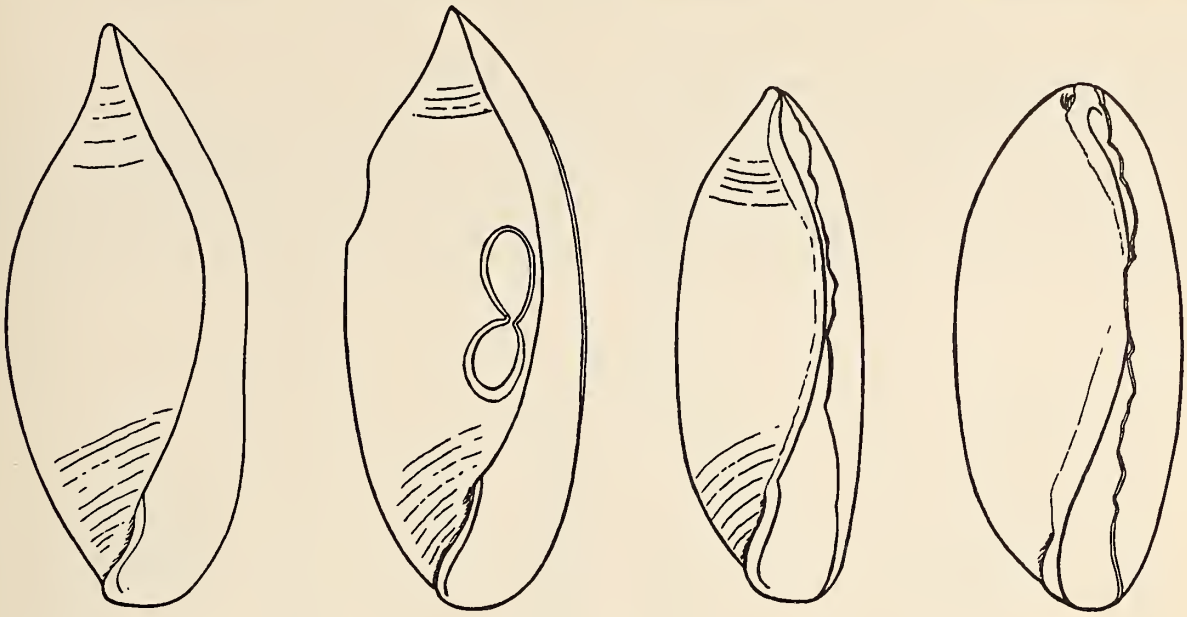

Figure 2 Figure 3 Figure 4 Figure 5

Figure 2: *Volvulella acuminata* (Bruguière). 3.94 mm high
Figure 3: *Volvulella acuminata* (Bruguière). England. 4.06 mm high
Figure 4: *Volvulella persimilis* (Mörch) (authentic specimen of *Volvulella oxytata* (Bush); 3.50 mm high)
Figure 5: Holotype of *Volvulella moerchi* Dall (= *V. persimilis* (Mörch)) 3.68 mm high

Pilsbry (1930) may have had only a single specimen available to describe *Volvulella ischnatracta*. It is completely spineless (broken?), but has an elongate form characteristic of this species, and spiral lines at both ends.

Volvulella recta (Mörch, 1875)

Bulla acuta d'Orbigny, 1842. Mollusca, *in* Sagra, Hist. . . . Cuba 1: 126; plt. 4, figs. 17 - 20. Type locality not specified; cited from Cuba, Jamaica, Guadaloupe and Martinique and "toutes les Antilles." *Non Bulla acuta* Grateloup, 1828, Bull. Hist. Nat. Soc. Linn. Bordeaux 2 (9): 87

Volvula recta "d'Orbigny" Mörch, 1875. Malak. Blätter 22: 179. Not figured. This fortuitous *lapsus calami* merely cites the page and illustration in d'Orbigny, 1842 of *Bulla acuta* d'Orbigny, but meets all requirements for rectifying d'Orbigny's homonym

Volvula minuta Bush, 1885. Trans. Conn. Acad. Sci. 6: 469; plt. 45, fig. 11. Type locality: off Cape Hatteras, N. Car., in 14 to 16 fathoms

Volvula bushii Dall, 1889. Bull. Mus. Comp. Zool. 18: 51. Not figured. Type locality: Station 2602, 36 miles S. ½ W. from Cape Hatteras, N. C., in 124 fathoms, sand. 1925, Dall, Proc. U. S. Nat. Mus. 66: 31; plt. 25, fig. 3

This, the first species in the genus to be described from the New World, had one of the most succinct descriptions and better illustrations of any from that area. The following is a free translation of d'Orbigny's description in French.

> "The shell is oblong, bright, thin, swollen in the middle, thinning at the extremities, marked in front by several spiral striations and behind by several others, a little in front of the extremity, which is transversely striate. Spire entirely enclosed, without umbilicus, replaced by a long, sharp prolongation. Aperture very straight, a little sinuate, prolonged behind, enlarged in front; columella a little projecting, separated by a groove from the umbilicus and forming a slight ridge. Color, uniformly white. Length 2 mm. Diam. ¾ mm."

He specifically called attention in both the Latin and French descriptions and in the discussion to the delicate, transverse, apical striae which are unique to this species. But he referred to them as longitudinal, using the term transverse for what is here termed spiral. The transverse striae are around the apical third of the shell and extend onto the base of the spine. They are very closely spaced,

regular, and somewhat stronger than growth lines. The greatest diameter of this species is above the midpoint of the length of the shell, in contrast to all others of the East Coast. The spine may be short and blunt, but the shell is never as solid in structure as that of *Volvulella paupercula*.

The U. S. National Museum has specimens from Cape Hatteras, North Carolina, and numerous ones from the Florida Keys. It extends into the Gulf of Mexico at least to Mobile, Alabama. These lots range in depth from 12 to 124 fathoms.

Figure 11 (USNM 44773, U. S. Fish Commission Station 2113, 15 fathoms, off Cape Hatteras, North Carolina) is drawn from a single shell of *Volvula minuta* BUSH which she sent to DALL. It is scarcely worn, and agrees closely with *Volvulella recta,* both in the shape and in having transverse striae at the apex. Spiral striae are

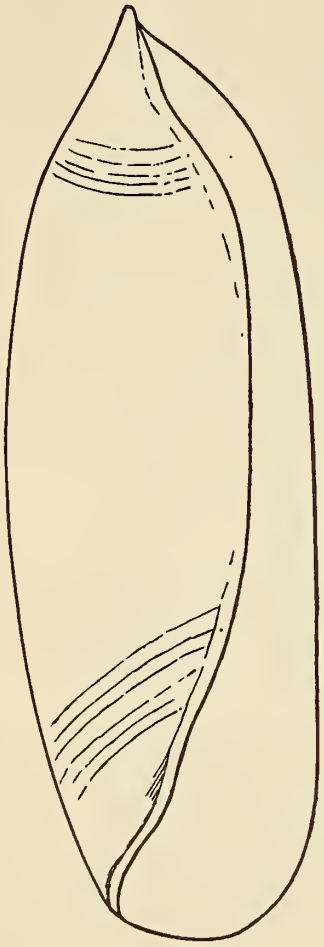

Figure 6

Figure 7

Figure 8

Figure 9

Figure 6: *Volvulella cylindrica* (CARPENTER). 6.19 mm high
Figure 7: Lectotype of *Volvulella cooperi* DALL (= *V. cylindrica* (CARPENTER)). 6.45 mm high
Figure 8: Lectotype of *Volvulella callicera* DALL (= *V. cylindrica* (CARPENTER)). 3.06 mm high
Figure 9: *Volvulella cylindrica* (CARPENTER). 7.88 mm high

Figure 10

Figure 11

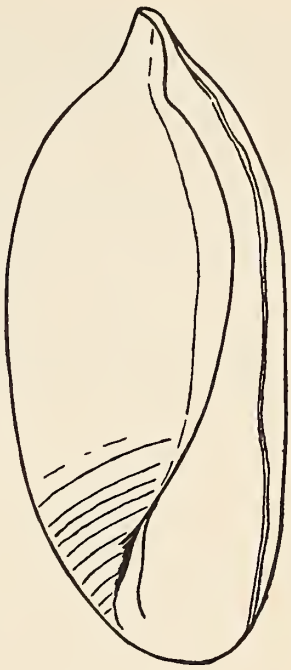

Figure 12

Figure 10: Lectotype of *Volvula bushii* DALL (= *Volvulella recta* (MÖRCH)). 4.31 mm high
Figure 11: *Volvulella minuta* (BUSH) (= *V. recta* (MÖRCH)). 2.02 mm high
Figure 12: Lectotype of *Volvulella californica* DALL. 4.44 mm high

strong at the apical end, less pronounced basally, and none could be detected on the midregion of the shell. It may be juvenile. Height 2.02 mm, diameter 0.92 mm.

Figure 10 (USNM 95301, off Cape Hatteras, North Carolina) is drawn from the larger of two specimens which are presumably cotypes of *Volvula bushii* DALL, 1889. It agrees most closely with the dimensions cited in the original description (DALL, 1889) "Lon. 4.6; Lat. 2.3 mm," and is here designated lectotype. He originally cited 6 specimens; there are no locality data with this lot, but the catalogue number is that which he cited in figuring the species (DALL, 1925).

Measurements of the two shells are:

	Height	Diameter
Lectotype:	4.31	2.06
Paratype:	3.25	1.56

Both shells are opaque, white, and slightly worn. They are quite characteristic of *Volvulella recta* in shape, having a very long, acute spine, and transverse striae at the apical end. Spiral striae are present at both ends, and microspirals are evident in the middle of the shell.

Volvulella paupercula (WATSON, 1883)

Cylichna (Volvula) paupercula WATSON, 1883. Journ. Linn. Soc. London 17: 325. Not figured. Type locality: Lat. 18° 38′ 30″ N., Long. 65° 05′ 30″ W., North of Culebra Island, St. Thomas, West Indies. 390 fathoms. 1886, WATSON, Challenger Report, Zoology, 15: 669 - 670; plt. 50, fig. 5

Volvula aspinosa DALL, 1889. Bull. Mus. Comp. Zool. 18: 51. Not figured. Type locality: "Off the North Carolina Coast in 18 to 168 fms., sand ... Straits of Florida, 150 - 200 fms." 1925, DALL, Proc. U. S. Nat. Mus. 66: 31; plt. 25, fig. 5

This species is somewhat more inflated than *Volvulella recta*. Larger specimens have the greatest diameter at the midpoint of the length, rather than above it. Transverse striae at the apical end are absent, although more widely spaced growth lines extending from apex to base are generally present. Coarse spiral striae are prominent at both ends, and fine spiral lines are often well shown in fresh shells. The spine is small, but usually absent. In the latter case the aperture does not quite reach the columella, although it bends strongly toward it at the apical end. A distinct but minute apical umbilicus is present in the

aspinous specimens. The shell is unusually thick for the genus. This may be a species which is reverting to a spineless condition. The general shape and sculpture, and presence of a distinct, short spine in some specimens, suggest it is truly a *Volvulella* rather than a *Cylichna*.

The species is well represented in the collection of the U. S. National Museum by material dredged by J. B. Henderson in 1917, on the yacht *Eolis*, along the Florida Keys and off Barbados. The range in depth is from 75 to 190 fathoms.

Figure 15 (USNM 95305, off Cape Hatteras, North Carolina) was drawn from the larger of two cotypes of *Volvula aspinosa* DALL, and is here designated the **lectotype.**

Measurements of the two shells are:

	Height	Diameter
Lectotype:	3.63	2.06
Paratype:	3.06	1.75

DALL (1925) cited USNM 95302 as the type lot, but I think that was a misprint. The type locality should be restricted to North Carolina. He gave the dimensions as "Long. 4.0; Lat. 2.0 mm." (DALL, 1889).

Figures 16 (height 3.63 mm, diameter 1.94 mm) and 17 (height 2.94 mm, diameter 1.50 mm) are drawn from specimens (USNM 500381) from 94 fathoms off Barbados, and show somewhat slimmer forms of this species.

Although *Volvulella paupercula* (WATSON) was described from shells taken at 390 fathoms, and thus much

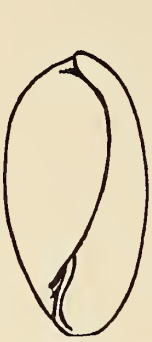

Figure 13

Figure 14

Figure 15

Figure 17

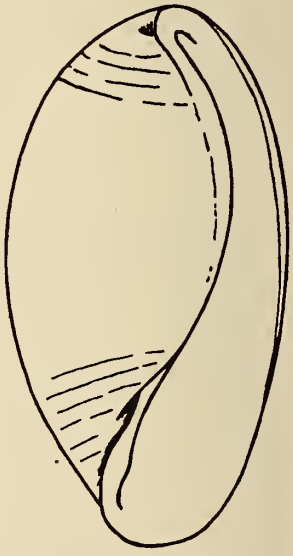

Figure 16

Figure 13: *Volvulella paupercula* (WATSON). Tracing of figure 5 of plate 50,
Figure 14: Lectotype of *Volvulella catharia* DALL. 2.75 mm high
Figure 15: Lectotype of *Volvula aspinosa* DALL
(= *Volvulella paupercula* (WATSON)). 3.63 mm high
Figure 16: *Volvulella paupercula* (WATSON). Barbados. 3.63 mm high
Figure 17: *Volvulella paupercula* (WATSON). Same lot as Figure 16. 2.94 mm high

deeper than any examined in the present study, the excellent description and detailed figure of it leaves little doubt that this is what DALL later named *Volvula aspinosa*. WATSON's figure has the sculpture more strongly indicated than it actually is. A tracing of his figure (without the sculpture) is here reproduced in Figure 13. The dimensions given by WATSON, converted from inches, are: height 1.55 mm, diameter 0.75 mm.

(Paravolvulella) HARRY, subgen. nov.

Type: *Volvulella (Paravolvulella) texasiana* HARRY, spec. nov.

This subgenus differs from the typical one in the more cylindrical form of the shell, with bluntly rounded rather than gently tapering shoulder; and especially in the deep, rounded sinus of the apical end of the outer lip, which appears in apertural view not to extend farther posteriorly than the base of the spine, rather than to its tip. However, the parietal lip does curve upward medial to the sinus to form the spine, which is short but acute.

There is a tendency for the species of this subgenus to be colored brown by iron stain (extrinsic coloration) in fresh specimens. This is unusual in marine mollusks. At Galveston, only a few of the off-shore species exhibit this phenomenon, whereas many others living under the same conditions are free of it.

Volvulella (Paravolvulella) texasiana HARRY, spec. nov.
(Figure 21)

Shell small, cylindrical, translucent, grey, flecked irregularly with opaque, white areas (growth interruptions), the ends washed with reddish brown (iron stain). Aperture as long as the single visible whorl, but exceeded slightly by the tip of the spine. Side of whorl and aperture flattened, or in larger shells very slightly constricted by a vague, broad, medial sulcus. The diameter of the shell is the same at both ends in larger shells, but in very young shells the outline is inflated, suboval, with the greater diameter in the middle. Apical and basal ends gently curved. The spine is short, though usually broken, with a minute, bilobed appearance when seen in profile, and a minute, deep pit in the spine when seen from above. There is a narrow spiral band of roughened shell material around the base of the spine, its outer edge slightly above the shell surface. This tapers out along the upper, truncate part of the outer lip. Outer lip roundly quadrate above, its inner end meeting the columellar axis at a right angle; it is thin, acute throughout its length. The edge of the outer lip forward of the posterior sinus is almost in one plane, but slightly more advanced in the direction of growth toward the base. Basal part of the lip strongly arched, not as advanced in the direction of growth as the outer. Columellar lip short, narrow, thickened, adnate, and without a lamella. No umbilicus, nor indentation in the umbilical area.

There are a few minute, closely and equally spaced spiral lines on the base, and similar, less prominent ones near the apical spine. Much fainter, wavy ones cover the middle part of the shell. These can only be seen at higher magnification.

Holotype: The holotype is USNM molluscan collection No. 678000, Height: 3.94 mm; Diameter 0.75 mm.

Type locality: Southeast of the base of the Bolivar Peninsula (east of Galveston, Texas), about 10 miles offshore, at 7 fathoms, Long. 94° 23′ W, Lat. 29° 22′ N. Two specimens were dredged there in December, 1965, and 4 more at the same place in January 1966, but no shells of this species were found in dredgings I examined from 54 other stations west and south of there, ranging from 3 to 18 fathoms. However, Mr. Charles Guice kindly provided specimens from three other stations (among 20 he examined) in the area. These yielded only one or two live animals per station. Two stations were at 7, and one at 9 to 10 fathoms. The species is evidently sparse and local.

Volvulella texasiana differs from *V. panamica* in its smaller size, in the slight medial constriction, and particularly in having a ridge around the spine. I could not find such a ridge in any specimens of *V. panamica* in the U. S. National Museum.

Species from the Eastern Pacific

The species of the west coast of North America have been most recently reviewed by J. Q. BURCH (1947), with many locality and depth records. He gave two keys, taken from the notebook of the late Dr. Strong, which rely chiefly on presence of spiral sculpture and height-diameter ratios of the shell.

Volvulella cylindrica (CARPENTER, 1864)

Volvula cylindrica CARPENTER, 1864. Reprt. Brit. Assoc. Adv. Sci. 1863, p. 537 and 647. Not figured. Type locality: Santa Barbara, California. 1958, PALMER, Geol. Soc. Amer. Memoir 76: 240; plt. 25, figs. 1, 2 (holotype, Redpath Museum, No. 2364; extensive references)

Volvulella cooperi DALL, 1919. Proc. U. S. Nat. Mus. 56: 297 - 298. Not figured. Type locality: Scammon Lagoon, Lower California

Volvulella callicera DALL, 1919. Proc. U. S. Nat. Mus. 56: 299. Not figured. Type locality: U. S. Fish Comm. Sta. 2813, off Galapagos Islands, in 40 fathoms, coral sand

Volvulella lowei STRONG & HERTLEIN, 1937. Proc. Calif. Acad. Sci. ser. 4, 22: 164-165; plt. 35, fig. 2. Type locality: Puerto Escondido, Gulf of California. 1939, STRONG & HERTLEIN, Allan Hancock Pacific Exped. 2 (12): 190; plt. 18, fig. 1 (specimen from Panama)

This is an elongate species closely related to *Volvulella acuminata* and *V. persimilis,* but it grows larger than either, and the sides are somewhat more flattened than in those species. The apical end of the aperture is not sinuate as in *V. panamica,* and it extends to the top of the spine in the same plane as the latter. The apical end of the shell tapers more gently than in that species. Broadly spaced spiral striae are present at both ends, those at the apical end being less prominent and more easily worn off. Finer, more closely spaced spiral lines are present on the midpart of the whorl of at least some non-worn specimens.

The spine is variable in length, but tends to be short with a broad base. Figure 6 (USNM 212655, largest of 4 specimens; height 6.19 mm, diameter 2.00 mm) was dredged from 5½ fathoms off Lower California, and has a more tapering spine than the holotype figured by PALMER (1958). The range of this species is generally cited as Vancouver Island to the Gulf of California (PALMER, 1958), but the U. S. National Museum has a lot of 2 shells (USNM 509036) from Panama, collected by Zetek, which are quite typical of this species.

Although GRANT & GALE (1931) and others have recognized *Volvulella cooperi* DALL as distinct, I think it is only an aspinous variant of this species. Figure 7 (USNM 105501, Scammon Lagoon, Lower California) was drawn from the next to smallest of 4 cotypes of *V. cooperi* DALL. All 4 are badly worn. Weak spiral lines are present on the bases of 2, but none could be found elsewhere. DALL evidently gave the measurements of the largest shell (9.5 mm long, diameter 3.6 mm) but both larger specimens are so badly worn as to make them poor choices for a type specimen. The one illustrated (Figure 7) is here selected as **lectotype**. It is only slightly worn, but the lip is badly broken.

Measurements of the cotypes are:

	Height	Diameter
Paratype:	9.68	3.61
Paratype:	7.61	2.58
Lectotype:	6.45	2.32
Paratype:	5.29	2.06

Figure 8 (USNM 194176 b) is drawn from the smallest of 3 cotypes (here designated **lectotype**) of *Volvulella*

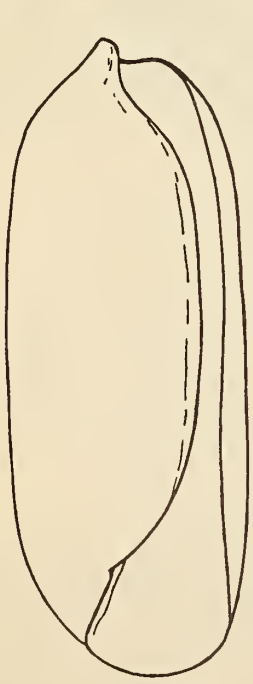

Figure 18

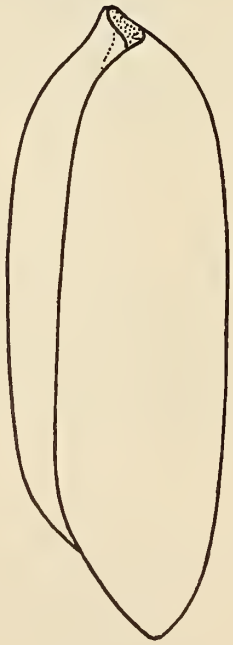

Figure 19

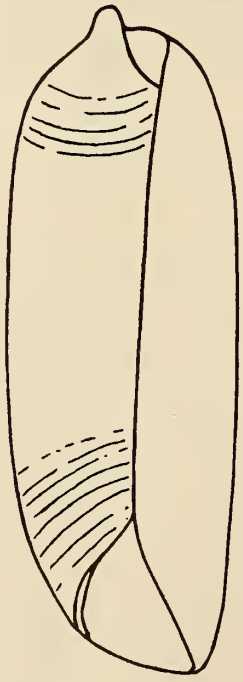

Figure 20

Figure 21

Figure 18: Lectotype of *Volvulella panamica* DALL. 4.25 mm high
Figure 19: Side view of the same shell as in Figure 18.
Figure 20: Paratype of *Volvulella tenuissima* WILLETT. 4.5 mm high
Figure 21: Holotype of *Volvulella texasiana* HARRY, spec. nov. 3.94 mm high

callicera DALL. All are bleached, with sand grains lodged in the aperture and the upper part of the lip slightly broken. But the sculpture is evident and quite typical: broadly spaced spiral lines at both ends, with finer, closely spaced lines in the middle. DALL (1919) gave the measurements: length 3.5 mm, diameter 1 mm.

My measurements of largest and smallest cotypes are:

	Height	Diameter
Paratype:	4.31	1.38
Lectotype:	3.06	0.94

Figure 9 (USNM 267574, Head of Conception Bay, Gulf of California) is drawn from a specimen set aside as "figured type" of a species to be named by BARTSCH. I can not find that he ever published it, although a manuscript name was present on several lots in the U. S. National Museum. They are a mixture of *Volvulella cylindrica* and *V. panamica,* all from the Gulf of California. The dimensions of the specimen drawn are: height 7.88 mm, diameter 1.69 mm.

I have seen no authentic specimens of *Volvulella lowei* STRONG & HERTLEIN, but judging from the figures and description, it is a poorly spined form of *V. cylindrica.*

Volvulella californica DALL, 1919

Volvulella californica DALL, 1919. Proc. U. S. Nat. Mus. 56: 299-300. Not figured. Type locality: off Santa Rosa Island, California, in 53 fathoms, sandy mud. 1927, OLDROYD, Marine shells west coast, 2 (1): 34; pl. 2, fig. 11 [poor]

Figure 12 (USNM 211303) is drawn from the larger (here designated **lectotype**) of 2 complete cotypes. A third cotype has the body whorl badly broken. The specimens are slightly weathered, so that there is no trace of finer spiral lines which may be present on unworn specimens. About 8 widely spaced spiral lines are present on the base of the lectotype, which shows none near the apex. Apical spirals are present in the complete paratype, however. The profile of the shell is broadly arched, with the greatest diameter in the middle. The spine is of moderate length. This may be the West Coast counterpart of *Volvulella recta,* but it lacks any trace of transverse striae near the apex. It is distinctly more cylindrical than that species. The only specimens I found in the U. S. National Museum which could certainly be referred to this species were those of the type series. Possibly this is only a growth stage of *V. cylindrica.* However, BURCH (1947) cites it from 6 stations, between Santa Cruz, California, and Todos Santos Bay, Lower California, ranging in depth from 30 to 298 fathoms. Measurements of 2 non-broken cotypes (*cf.* DALL, 1919, who stated "length 4; diameter 1.7mm") are:

	Height	Diameter
Lectotype:	4.44	2.00
Paratype:	3.63	1.56

Volvulella catharia DALL, 1919

Volvulella catharia DALL, 1919. Proc. U. S. Nat. Mus. 56: 298. Not figured. Type locality: U. S. Fish. Comm. Sta. 2794 in Panama Bay, in 62 fathoms, sand

Figure 14 (USNM 211784) is a drawing of the slightly more globose of the 2 non-broken of 4 cotypes, all of which are about the same size and slightly worn. It is here designated **lectotype.** It measures: height 2.75 mm, diameter 1.44 mm (DALL, 1919, stated: "length of shell, 2.75; diameter, 1.8 mm"). This is the West Coast counterpart of *Volvulella paupercula* (WATSON), and the limited series at the U. S. National Museum (only one other lot, 194976a, Galapagos Islands, 40 fathoms) leaves room for doubt about whether it is distinct from that species. It may not grow as large as the eastern one. A few widely spaced spiral lines are present on the base, but none could be seen on the apex, nor over the midregion of the shell (worn off?). It is very thick shelled, like its eastern relative, and there is no spine, but a minute, rimate umbilicus at the apex.

Volvulella (Paravolvulella) panamica DALL, 1919

Volvulella panamica DALL, 1919. Proc. U. S. Nat. Mus. 56: 298. Not figured. Type locality: Panama Bay at Sta. 2799, in 29½ fathoms. 1937, STRONG & HERTLEIN, Proc. Calif. Acad. Sci. ser. 4, 22: 164; plt. 35, fig. 3

Volvulella tenuissima WILLETT, 1944. Bull. So. Calif. Acad. Sci. 43: 71-72; plt. 4. fig. 1. Type locality: Off Redondo, California, in 75 fathoms

Figures 18 and 19 are drawn from the single shell in a separate vial of USNM 212654, height 4.25 mm, diameter 1.56 mm (DALL stated: "length 4.25, diameter 1.75 mm") which is here designated **lectotype** of *Volvulella panamica* DALL. Another vial with the same catalogue number contains a large series of specimens, all slightly weathered. The lectotype has traces of strong spiral lines at both ends, and finer, closely spaced ones over the middle. This is the most distinctly cylindrical of the West Coast species, with the apical end abruptly rounded, the spine short and blunt, and the apical end of the lip deeply sinuate by not being as advanced in the direction of growth as the rest of the lip. The apical part of the lip appears truncate, not extending to the tip of the spine, although the parietal wall actually forms the latter (Figure 19).

Figure 20 is drawn from the larger of 2 perfect (of 3) paratypes of *Volvulella tenuissima* Willett (USNM 573516, height 4.50 mm, diameter 1.63 mm). The specimens were evidently collected alive, and show pronounced sculpture, with brown iron stain on the ends. The spiral lines on the ends are very closely spaced, but I suspect this varies within the species. It is notable that Willett (1944) compared his new species only with *V. cylindrica* and did not mention *V. panamica*. This species ranges from off Redondo, California, to Panama, and is abunddantly represented in the U. S. National Museum from the Gulf of California. There is no apical spiral ridge in any of the numerous specimens seen of *V. panamica*, such as that present in *V. texasiana*.

Species of the Indian and Western Pacific Oceans

Listed below in alphabetical order are all trivial names I have found of living species of this genus in the western Pacific and Indian Oceans. This includes 3 which have been attributed to the genus, but probably belong elsewhere, and one which was described as *Cylichna* which probably is a *Volvulella*. Further studies on this genus in the Indo-Pacific area should review all those described as *Cylichna*, for possibly others originally so allocated belong here. Populations very similar to *V. acuminata* are widely distributed in these oceans. Whether they are specifically distinct from that species is a moot question. But one of them, *V. pia*, was described from the southern tip of Africa and might as well be relegated to the Atlantic as to the Indo-Pacific fauna. The other 3 species groups of American shores are found in these oceans also. I have made a guess regarding the Atlantic analogue of each nominal species listed below. The species described by A. Adams in 1862 are particularly difficult to recognize, being described in a few lines of Latin, not figured, and with no measurements. Some authors have named new species if they found them at a distance, or of an age, remote from any species previously described. Insufficient specimens from the Indo-Pacific have prohibited decisions on the validity of these, but I have pointed out such opinions on synonymy as have been found.

acutaeformis Yokoyama, 1922 (*Volvula*), p. 26, pl. 1, fig. 9. Type locality: fossil, from Shito, Japan (of *V. recta* group; he compared it to *V. minuta* Bush). Kuroda & Habe (1952) attributed it to the recent fauna of Japan, and Habe (1954) declared it a synonym of *V. ovulina* Adams.

angustata A. Adams, 1850 (*Bulla (Volvula)*), p. 596, pl. 125, fig. 153. Type locality: Cagayan, Mindanao (Philippines), 25 fathoms (of *V. acuminata* group).

aomoriensis Nomura, 1939 (*Rhizorus*), p. 26, pl. 2, figs. 9a, 9b. Type locality: Japan, numerous localities cited, 30 fathoms (of *V. acuminata* group). Habe (1955) called this a synonym of *V. radiola* Adams.

artiaperta Yamakawa, 1911 (*Volvula*), p. 50, pl. 11, figs. 33 - 36. Type locality: fossil, Japan [original not seen]. Kuroda & Habe, 1952, cited this living, and Habe, 1955, said it is a synonym of *V. eburnea* Adams.

attenuata A. Adams, 1862 (*Volvula*), p. 155, not figured. Type locality: Tsu-Sima (Japan), 26 fathoms. (Probably of *V. recta* group).

compacta Melvill, 1906 (*Volvula*), p. 79, pl. 7, fig. 26. Type locality: not indicated, evidently Persian Gulf or Gulf of Oman. No depth given (of *V. paupercula* group).

cylindrella A. Adams, 1862 (*Volvula*), p. 155, not figured. Type locality: Mino-Sima (Japan), 63 fathoms (of *V. acuminata* group).

eburnea A. Adams, 1850 (*Bulla (Volvula)*), p. 597, pl. 125, fig. 155. Type locality: China Sea. Kuroda & Habe (1954, pl. 2, fig. 11) provided a photograph of a specimen supposedly identified by Adams, now in the Redpath Museum (probably of *V. recta* group).

exilis Thiele, 1925 (*Volvula*), p. 316, pl. 31, fig. 25. Type locality: Padang, Sumatra (a poorly spined specimen of the *V. acuminata* group).

flavotincta Martens, 1903 (*Volvula*), pp. 130-131, pl. 5, fig. 21. Type locality: East Africa, (Valdivia) station 270, in Gulf of Aden, 1840 m deep (possibly of the *V. paupercula* group).

fortis Thiele, 1925 (*Volvula*), p. 238, pl. 31, fig. 23. Type locality: 0° 30.2′ N Lat., 97° 59.7′ E Long., 132 m depth, "Nias-Süd Kanal" (South of Sumatra) (probably of *V. recta* group; it has transverse ridges at the base of the spine).

granulum Philippi, 1851 (*Bulla*), pp. 63-64; not figured. Type locality: China. This is probably the "*granulum* Philippi" listed under *Volvula* by H. & A. Adams (1854: 14). I agree with Pilsbry (1893: 309), who placed it in *Cylichna*.

kinokuniana Habe, 1946 (*Rhizorus*), p. 186, not figured. The description is in Japanese. Kuroda & Habe (1954, pp. 8-9, pl. 2, fig. 15) illustrated a shell in the Redpath Museum, supposedly received from A. Adams, under the unpublished name *Volvula solidula* A. Adams. They declared this is *Volvuella* [sic] *kinokuniana* Habe and note the species is from "deep bottoms of Tosa Bay, Shikoku, and also off Wakayama Pref., Honshu (Japan)" (of *V. paupercula* group).

lenis Thiele, 1925 (*Volvula*), p. 238, pl. 31, fig. 22. Type locality: 0° 39.2′ S Lat., 98° 52.3′ E Long., 750 m

depth, near Siberoet Island (South of Sumatra) (of *V. paupercula* group).

mecyntea MELVILL, 1912 (*Cylichna*), p. 253, pl. 11, fig. 15. Type locality: Persian Gulf, Ormara. The single specimen was spineless, but seems to be a *Volvulella* of the *V. texasiana* group.

minutissima THIELE, 1925 (*Volvula*), p. 316, pl. 31, fig. 24. Type locality: (*l.c.*, p. 254): Padang, Sumatra (of *V. recta* group; it has transverse ridges at the base of the spine).

mucronata PHILIPPI, 1849 (*Bulla*), p. 22, not figured. Type locality: Red Sea at Aden. This is probably the *mucronata* PHILIPPI listed by H. & A. ADAMS (1854: 14) under *Volvula*, and cited by A. ADAMS (1862). I agree with PILSBRY (1893: 191), who placed it in *Tornatina*.

nesentus FINLAY, 1926 (*Rhizorus*), p. 438; new name for *Volvulella reflexa* SUTTER, 1913 (p. 529, pl. 23, fig. 2; Recent of New Zealand, *non Cylichna reflexa* HUTTON, 1886, fossil, Miocene of New Zealand).

opalina A. ADAMS, 1862 (*Volvula*), p. 154, not figured. Type locality: Mino-Sima, 63 fathoms (Japan) (possibly of *V. acuminata* group).

ovulina A. ADAMS, 1862 (*Volvula*), p. 155, not figured. Type locality: Mino-Sima, 63 fathoms (Japan) (probably of *V. recta* group).

parata IREDALE, 1936 (*Volvulella*), p. 332. New name for a figured specimen HEDLEY (1903: 394, fig. 109) had identified as *V. rostrata* A. ADAMS. DELL (1956) argued convincingly that this is merely a synonym of *V. rostrata*.

pia THIELE, 1925 (*Volvula*), p. 238, pl. 31, fig. 21. Type locality: 34° 51′S Lat., 19° 37.8′ E Long., 80 m, near Cape Agulhas (Southern tip of Africa) (similar to *V. acuminata*, of which it may be a synonym).

radiola A. ADAMS, 1862 (*Volvula*), p. 155, not figured. Type locality: Tabu-Sima, 25 fathoms (Japan). The description suggests it belongs to the *V. acuminata* group, but KURODA & HABE (1954, pl. 2, figs. 3 and 4) published a photograph of a shell in the Redpath Museum supposedly from A. ADAMS, which resembles the *V. texasiana* group.

rostrata A. ADAMS, 1850 (*Bulla (Volvula)*), p. 596, pl. 125, fig. 154. Type locality: Port Lincoln (Australia) (probably of *V. recta* group).

spectabilis A. ADAMS, 1862 (Volvula) p. 154, not figured. Type locality: Tabu-Sima, 25 fathoms (Japan) (probably *V. acuminata* group).

striatula A. ADAMS, 1850 (*Bulla (Volvula)*), p. 597, pl. 125, fig. 156. Type locality: China Sea (possibly of *V. texasiana* group).

sulcata WATSON, 1883 (*Cylichna (Volvula)*), p. 326, not figured. Type locality: Torres Strait, North of Australia. WATSON, 1886, p. 670, pl. 50, fig. 6 (of *V. recta* group).

tokunagai MIKIYAMA, 1927 (*Volvulella acuminata* subspec.), pp. 144-145, not figured. New name for the Japanese Pleistocene fossil *Cylichna acuta* "D'ORB." TOKUNAGA, 1906, Journ. Coll. Sci. Univ. Tokyo 21 (2): 32, pl. 2, fig. 13, not *Bulla acuta* D'ORBIGNY. NOMURA (1939: 26) elevated this subspecies to specific rank, and cited it living at several localities in Japan. NOMURA's figures (*l. c.*, pl. 2, figs. 8 a, 8 b) show it belongs to the group of *V. recta*.

tragula HEDLEY, 1903 (*Volvula*), p. 395, text fig. 110. Type locality: 63-75 fathoms, off Port Kembla, Australia (resembles *V. recta*; there are coarse spiral ridges at the base of the spine shown in the figure but not mentioned in the text).

truncata DELL, 1956 (*Volvulella*), p. 146, pl. 20, figs. 211, 212. Type locality: 260 fathoms, Chatham Islands, New Zealand (possibly of *V. texasiana* group).

SUMMARY

Volvulella, a genus of minute snails, is world wide in distribution in the tropics and warm temperate waters, ranging from a few to many meters depth. They are rare and local, with few distinctive characters to distinguish species. Four species groups are recognized, with analogous species in the various major oceans. Possibly only one species group occurs in the eastern Atlantic, but all 4 groups are represented in the western Atlantic and eastern Pacific, and in the Indo-Pacific area. *Volvulella* NEWTON, 1891, is accepted as the correct name of this genus, of which *Bulla acuminata* BRUGUIÈRE is the type species by designation of A. ADAMS, 1862. *Paravolvulella*, new subgenus is established with *V. (P.) texasiana*, spec. nov., designated as type. Six unfigured type specimens of nominal species of DALL from the east and west coast of North America are illustrated. A catalogue of 30 nominal species from the Indo-Pacific area indicates to which of the 4 recognized species groups each may belong.

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